and asymmetric cell division, keeping centrosome size under tight control is clearly not a bad idea!

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DOI: 10.1016/j.cub.2010.11.032

Social Cognition: Feeling Voices to Recognize Emotions

Our understanding of how we simulate other people's actions and feelings to recognize their emotional states is extended by a new study which finds that premotor and somatosensory cortices are required to process the emotional meaning of sounds.

Ralph Adolphs

Do we know what we think or intend by observing what we say or do? The novelist E.M. Forster and painter Robert Motherwell thought so, and William James popularized it for the case of emotions as well, which he thought of as bodily expressions that we come to know about by feeling them. Cognitive neuroscience has provided considerable support for this view and shown that we can use the same mechanism also to know the emotions of others: recognizing emotions from looking at somebody's facial expressions has been shown to require the somatosensory cortices [1,2].

A new piece of the puzzle has now been provided by Banissy *et al.* [3], whose work shows that somatosensory and premotor cortices are required also to recognize emotion from nonverbal auditory stimuli. The finding is important for several reasons. First, it demonstrates the ubiquity of a 'simulation' mechanism in understanding other people's emotions, whether it be from body postures, facial expressions, or voice. Second, in showing anatomical overlap with regions also known to participate in recognizing emotions from facial expressions, it suggests that there may be a modality-independent representation of emotion in somatomotor cortices: they form the substrate of our very concept of emotions. Third and relatedly, it seems unlikely that somatomotor cortices are merely representing the way somebody's vocal tract and mouth feel when they are producing emotional sounds. Instead, activity in these regions may comprehensively represent the state of the body of somebody experiencing the emotion associated with the sound. While prior studies [4,5] have broadly suggested that right frontoparietal cortices are required for auditory emotion recognition, they used different types of stimuli (prosody in speech) and did not yet find a clear role for somatosensory cortex.

The new experiment [3] used a particular type of transcranial magnetic stimulation (TMS), continuous theta-burst stimulation, to reduce neural activity over the right premotor and postcentral cortex for a few minutes. During that time, participants were asked to judge if two emotional voices expressed the same emotion or not (four emotions were used: amusement, sadness, fear, or disgust). TMS resulted in longer

reaction times on this task, demonstrating that processing was compromised. The impairment was not seen when the judgment was about the identity of the person from the voice, even when such identity judgments were made quite sensitive and difficult in a separate task. By using TMS, the authors were able to conclude that somatomotor cortices have a causal role in vocal emotion recognition.

The results lack the resolution to determine whether there are so-called 'mirror neurons' in the regions responsible for the effect: do the same neurons represent our own emotional states and those of others? Mirror neurons were first defined as cells that fire during a monkey's execution of a goal-directed action and its observation of another monkey or person performing the identical action. Such cells have recently been found in the human brain as well, and they appear to be present, albeit in relatively low proportion, in many cortical regions and to respond to many different kinds of actions, including those that constitute emotional expressions [6].

Are the present results specific to nonverbal vocal emotional stimuli? A lesion study [4] investigating emotion recognition from prosody (the emotional modulation of speech) also found right premotor regions to be critical, but failed to find a clear role for right somatosensory cortex; another study [7] found that lesions to right somatosensory cortex impaired the ability to experience emotions from music, but only slightly reduced the ability to recognize the intended emotion. A number of studies all support the idea that emotion recognition from a variety of stimuli (facial expressions, body postures, prosody) involve right somatosensory cortices, but other brain regions are also variably involved [8]. This heterogeneity, together with the typically correlational results from using methods such as functional magnetic resonance imaging (fMRI), leave it an important open question which brain structures are required to process particular modality-dependent types of emotional signals, and which are truly multimodal.

It remains unclear at what point in time sensorimotor cortices come into play. TMS either to premotor cortex or to somatosensory cortex resulted in equivalent disruption of emotion recognition in Banisy *et al.'s* study [3], suggesting that both action and sensory representations are required when we simulate another person's emotional state; one would expect them to be engaged in sequence. For instance, studies using magnetoencephalography have suggested that somatosensory cortices may come online around 300 ms after stimulus onset, once considerable sensory processing has been achieved and the stimulus has been associated with its emotional valence to some degree [9]. There is also the need for a more fine-grained anatomical mapping — current views argue that only somatosensory cortical areas BA1 and BA2 (as well as secondary somatosensory cortex) are engaged when we simulate others, whereas BA3 (primary somatosensory cortex) may be dedicated to representing only actual sensations at one's own body surface [10].

There are several further questions raised by the new study [3]. While reaction times were altered by the TMS as described above, accuracy on the task was unchanged. This may suggest that disruption of somatomotor cortices was incomplete; it may also suggest alternative, slower mechanisms through which we can figure out how people feel, raising a challenge for how to view 'simulation' accounts. Are they the whole story, a big part of the story, or a small part of the story? If they are less than the whole story, a further question is whether different people rely on simulation to varying degrees. Perhaps simulation is one strategy amongst many to gain knowledge of others' emotions, and perhaps there are individual differences in the extent to which this particular strategy is deployed. This will be an important direction for future studies, especially in light of findings that this mechanism is compromised in certain disorders, such as autism [11].

Another recent study suggests [12] that there may be at least one other set of processes: vocal, facial, and body-posture expressions of emotion were all found to activate sectors of medial prefrontal cortex and superior temporal sulcus, regions thought to mediate 'theory of mind'. Taken together, the two studies [3,12] resurrect older debates in philosophy and psychology about whether we use more abstract reasoning or simulation to figure out the internal states of other people. As is usual in such debates, the answer is likely to be 'both', and neuroscientists will be kept in business by figuring out to what extent, under what conditions, and for what personality of the perceiver.

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DOI: 10.1016/j.cub.2010.11.019